

EFFECT OF POSITION WITH RESPECT TO TREEFALL GAP ON DEGREE OF PLANT HERBIVORY

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Abstract: Canopy gaps formed by treefalls influence the light environment experienced by saplings, which may in turn influence sapling resistance to herbivores. However, the direction and magnitude of the effect depends on the nature of phenotypic responses of saplings to light. Plants might adjust secondary metabolism to optimize the benefits of defense relative to the costs of diverting resources away from growth (optimal allocation model). In this case, plants in gaps should experience the highest levels of herbivory. Alternatively, if secondary metabolism is simply a function of the amount of carbon in excess of that which can be used for growth (carbon surplus model), then plants in the understory, which are limited by light, should have less carbon to allocate to secondary metabolism, and sustain the highest herbivory. We measured herbivory in four plant species that inhabit gaps of the lower montane rain forest near Monteverde: *Psychotria elata* (Rubiaceae), *Psychotria aubletiana* (Rubiaceae), *Ossaea micrantha* (Melastomataceae), and *Razisea spicata* (Acanthaceae). For all species, herbivory decreased from gap center to forest canopy. This matches the patterns of genetic variation among tree species adapted to gaps vs. understory and suggests that anti-herbivore defenses are optimized and regulated, rather than determined by physiological constraints.

Key Words: phenolics, plant defense, resource allocation

INTRODUCTION

Canopy gaps formed by treefalls play an important role in determining the vegetative composition in forests. The gaps provide higher light habitat than the forest understory, which permits colonization by tree species that cannot survive below a closed canopy. Coley (1983) suggested a model to explain interspecific differences in resource allocation to growth vs. defense between gap-colonizing species and canopy species. Under this model, gap-adapted species rely on rapid growth to outcompete each other for limited light and space. In contrast, species or genotypes adapted to relatively low-light environments at the periphery of gaps and in adjacent forest are predicted to have low intrinsic growth rates and invest proportionately more energy in defense against herbivory (Sagers and Coley 1995).

In addition to genetic variation, many plants also exhibit high phenotypic plasticity in their allocation of resources to defense. Environmental effects on plant phenotypes could produce the same pattern of

antiherbivore defense across light gradients as does genetic variation among the species that tend to occupy gaps vs. understories. This might be expected if natural selection has shaped plant responses to environmental variation so that allocation to defense vs. growth is optimized with respect to local environments. Alternatively, plant secondary metabolism may be a byproduct of environmental effects on the amount of carbon that cannot be invested in growth because of other resource limitations (especially water or mineral nutrients; Coley 1993). In the first case (optimal allocation model), individuals growing in the understory should be better defended than conspecific individuals growing in a gap. In the second case (carbon surplus model), the opposite pattern should hold. We tested these alternative hypotheses by comparing levels of herbivory on four common plant species across a gradient from gap center to forest canopy.

METHODS

This study was conducted on 21 - 22

January 2000 in four similarly-aged (new growth 1-3 m high) gaps in the lower montane rain forest (1675 - 1775 m elevation) north-east of the Monteverde Estación Biológica, Monteverde, Costa Rica. Herbivory was examined in four plant species that were common along the light gradient from the gaps to understory: *Psychotria elata* (Rubiaceae), *Psychotria aubletiana* (Rubiaceae), *Ossaea micrantha* (Melastomataceae), and *Razisea spicata* (Acanthaceae). We sampled in three positions along the light gradient within each gap: gap center, gap edge, and under the canopy. The gap was defined as the area with no canopy cover directly overhead. Gap edge was defined as the trees within 5 m of the canopy gap, and canopy as the next 5 m into the understory. At each position, we randomly placed a 5 m transect perpendicular to the mountain slope, along which we randomly sampled up to nine representative plants (or as many as were present) within each species. On six randomly chosen leaves of each plant (excluding the top four leaves to control for possible effects of leaf age), we estimated the percent of leaf area lost to herbivory in 5 categories: 1 = no herbivory, 2 = 1-10% lost, 3 = 11-20% lost, 4 = 21-30% lost, 5 = >31% lost.

We used a two-way ANOVA, followed by Tukey-Kramer pairwise comparisons ($P = 0.05$), to test for effects of plant species and gap position on herbivory level.

RESULTS

Herbivory decreased from gap center

Table 1. Results of ANOVA testing for effects of plant species and gap position on leaf herbivory.

Source	d.f.	MS	F	P
position	2	136.56	57.34	<0.0001
species	3	74.84	31.44	<0.0001
position x species	6	3.53	1.48	0.18
Plant [position, species]	283	2.38	3.32	<0.0001

to forest canopy for *P. elata*, *P. aubletiana*, and *O. micrantha* (Table 1, Fig. 1). *R. spicata* suffered greater herbivory than the other three species in all gap positions (Table 1, Fig. 1) and equally high herbivory in edge and gap positions (Tukey-Kramer comparisons). There was no interaction between plant species and gap position (Table 1, Fig. 1).

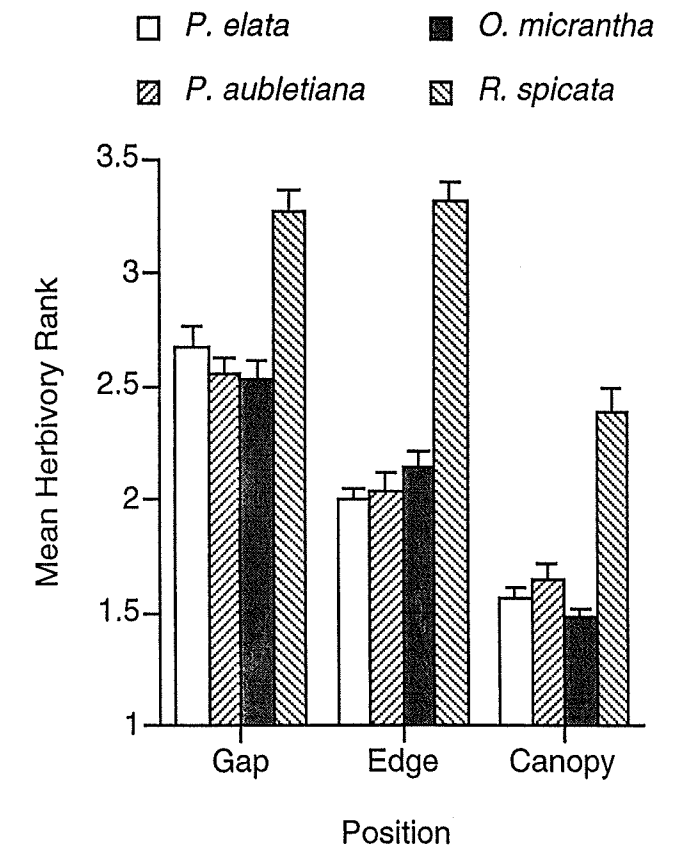


Figure 1. Effect of gap position on herbivory level (mean ± SE) of four plant species in a tropical montane forest. Herbivory ranks 1 to 5 correspond to leaf loss of 0%, 1 - 10%, 11 - 20%, 21 - 30%, and ≥ 31%, respectively.

DISCUSSION

Levels of herbivory were higher in the gaps than in the forest understory, which suggests that understory trees are better defended against herbivores than gap trees of the same species just a few meters away. These differences are probably not due to genetic differences, so it appears that patterns of phenotypic plasticity in antiherbivore defenses across light gradients at Monteverde match the patterns of genetic variation in plant defenses (Coley 1985). This phenotypic plasticity can be interpreted as an adaptive adjustment of allocation strategies (optimal allocation model) by the same reasoning that Coley (1985) used to explain genetic differences between gap species and understory species. In contrast, the observed phenotypic pattern in herbivory is exactly the opposite that would be expected under models of phenotypic variation in plant defenses that emphasize physiological constraints, rather than optimal allocation (carbon surplus model).

An alternative explanation for the correlation between gap position and herbivory level is that herbivorous arthropods are more abundant in treefall gaps than in the forest canopy (Berry 1994). This could result if plants that occur in gaps experience higher herbivory than plants of the same species that occur in understory habitats, regardless of their allocation to growth vs. defense. Direct measurements of arthropod abundance and/or plant secondary metabolites would be useful in distinguishing between these very different explanations for the differences in leaf herbivory between gaps and understory.

R. spicata experienced the highest herbivory levels in each position along the light gradient, indicating that it might allocate lower amounts of energy to defense than the other species. Based upon this pattern, Coley's model of interspecific variation in plant defenses would predict that *R. spicata*

also has a higher maximum growth rate than the other species and is more strongly restricted to gaps than the other species.

Phenotypic patterns in herbivores from canopy to gap center were strikingly similar between species. This gradient in herbivore pressure across the light gradient could influence patterns in species composition from the canopy to the gap, and therefore influence the diversity of plant life within the forest as a whole.

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